Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2009) **18**, 724–734

RESEARCH PAPER

Predation has a greater impact in less productive environments: variation in roe deer, *Capreolus capreolus*, population density across Europe

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ABSTRACT

Aim We aimed to describe the large-scale patterns in population density of roe deer *Caprelous capreolus* in Europe and to determine the factors shaping variation in their abundance.

Location Europe.

Methods We collated data on roe deer population density from 72 localities spanning 25° latitude and 48° longitude and analysed them in relation to a range of environmental factors: vegetation productivity (approximated by the fraction of photosynthetically active radiation) and forest cover as proxies for food supply, winter severity, summer drought and presence or absence of large predators (wolf, *Canis lupus*, and Eurasian lynx, *Lynx lynx*), hunter harvest and a competitor (red deer, *Cervus elaphus*).

Results Roe deer abundance increased with the overall productivity of vegetation cover and with lower forest cover (sparser forest cover means that a higher proportion of overall plant productivity is allocated to ground vegetation and thus is available to roe deer). The effect of large predators was relatively weak in highly productive environments and in regions with mild climate, but increased markedly in regions with low vegetation productivity and harsh winters. Other potentially limiting factors (hunting, summer drought and competition with red deer) had no significant impact on roe deer abundance.

Main conclusions The analyses revealed the combined effect of bottom-up and top-down control on roe deer: on a biogeographical scale, population abundance of roe deer has been shaped by food-related factors and large predators, with additive effects of the two species of predators. The results have implications for management of roe deer populations in Europe. First, an increase in roe deer abundance can be expected as environmental productivity increases due to climate change. Secondly, recovery plans for large carnivores should take environmental productivity and winter severity into account when predicting their impact on prey.

Keywords

***Capreolus capreolus*, forest cover, lynx, population density, red deer, roe deer, top-down control, vegetation productivity, winter harshness, wolf.**

DOI: 10.1111/j.1466-8238.2009.00480.x

INTRODUCTION

Most species of herbivorous mammals are elements of food webs occurring over enormously wide gradients of environmental productivity. In Europe, the three most common species of large herbivores (the roe deer, *Capreolus capreolus* L., the red deer, *Cervus elaphus* L., and the fallow deer, *Dama dama* L.) inhabit a wide range of habitats from Mediterranean to boreal biomes (Mitchell-Jones *et al.*, 1999). Determining whether their densities are shaped by plant resources or predation seems especially urgent. An increase in ungulate numbers in Europe has been observed in recent decades (e.g. Andersen *et al.*, 1998a), and wildlife managers are becoming increasingly interested in the reintroduction and natural recovery of large carnivores as a potential remedy for overabundance of deer (e.g. Hetherington & Gorman, 2007) and in the potential negative impact that predators may have for sustainable hunter harvest of ungulate populations (Andersen *et al.*, 2007).

However, despite the growing interest in multi-trophic level investigations, ecologists studying large mammals face difficulties in applying food web theories to real world examples. There have been very few empirical studies so far, and these have yielded contradictory results. Crête (1999) found support for a strong top-down limitation of herbivores when analysing deer biomass along a biogeographical gradient in North America. In the Serengeti, Tanzania, populations of large ungulates exhibited food limitation, whereas small-sized ungulates (body mass below 150 kg) experienced strong predation (Mduma *et al.*, 1999; Sinclair *et al.*, 2003). In a European temperate forest, a long-term local study on the ungulate community suggested that both top-down and bottom-up control were at work, with predation exerting a stronger effect on ungulate populations when climate was most unfavourable (Jędrzejewska & Jędrzejewski, 2005).

In this paper, we analysed variation in roe deer population density from 72 localities spanning 25° latitude and 48° longitude in Europe in relation to a range of environmental factors including vegetation productivity and forest cover (as proxies for food supply), winter severity, summer drought and the presence or absence of large predators (wolf, *Canis lupus* L., and Eurasian lynx, *Lynx lynx* L.), hunter harvest and a competitor (the red deer).

The present distribution of our model species ranges from the Mediterranean shrublands of southern Spain to the boreal forest of central Norway, and from Britain to Russia (Linnell *et al.*, 1998). Throughout their range, roe deer are influenced by a wide array of factors. Large carnivores, mainly Eurasian lynx and wolf, regularly prey on roe deer in many parts of Europe (Filonov, 1989; Jędrzejewski *et al.*, 1993, 2002; Okarma, 1995; Jobin *et al.*, 2000; Mattioli *et al.*, 2004; Odden *et al.*, 2006). The roe deer's food supply can be altered by changes in agricultural and forestry practices and by competition with other wild ungulates such as red deer (Latham *et al.*, 1996). Most populations are subject to hunter harvest and some of them to supplementary winter feeding. Abiotic factors such as snow may have dramatic effects on roe deer population dynamics (Grøtan *et al.*, 2005).

We proposed that the same set of factors, although differing in strength, control roe deer population at both local and biogeographical scales. Specifically, we expected that: (1) with spatially decreasing environmental productivity, there will be a lower carrying capacity of the habitat for roe deer, and thus lower densities of the species; (2) predators – wherever present – will be a limiting factor for roe deer populations in the whole range of the species, but stronger limitation is expected in less productive (low food) environments and in regions with harsh climate.

MATERIALS AND METHODS

We collected published (obtained through a literature search) and unpublished data (from various research projects conducted by the authors of this paper) on the autumn–winter population density values (i.e. the number of animals per unit area) of roe deer in 72 locations in Europe (Fig. 1) from 1961 to 2005 (see list of data and sources in Table S1 in Supporting Information). We used mean values if the data were available for more than 1 year or were given as a range. Population numbers reported in the analysed sources had been given by diverse methods with different levels of accuracy: drive census (18 localities), vantage-point observation (17), pellet-group count (11), snow tracking (9), capture–mark–recapture (6) and other (3). Some papers (8) did not report the method (see Table S1).

We related the density values of roe deer to indices of vegetation productivity, forest cover, winter harshness, summer drought, the presence/absence of hunting, large predators (wolf and Eurasian lynx) and a potential competitor (red deer). To calculate the vegetation productivity index, we used monthly 4×4 km MODIS FPAR data sets covering January 2000 to June 2006 (obtained from the MODIS and MISR site at Boston University; http://cliveg.bu.edu/modismisr/). The fraction of photosynthetically active radiation (FPAR) represents the percentage of radiation available for photosynthesis which is absorbed by vegetation (Myneni *et al.*, 2002). The annual mean FPAR is higher in areas with high productivity. For some of the locations, winter FPAR values for the years 2001–03 were not available, so we used values for July 2003 to June 2006. The mean FPAR values were calculated for a circular area (radius 10 km, area about 314 km^2) around each location. We expected that area to be large enough to account for all the variance in productivity in a particular location.

We used the MODIS Vegetation Continuous Fields (VCF; Hansen *et al.*, 2002) tree cover data, available at http://edcdaac.usgs.gov/, as a measure of percentage forest cover in the study areas. These data have a spatial resolution of 500 m. We chose the same buffer size as with FPAR data (10-km radius around the centre of each study site).

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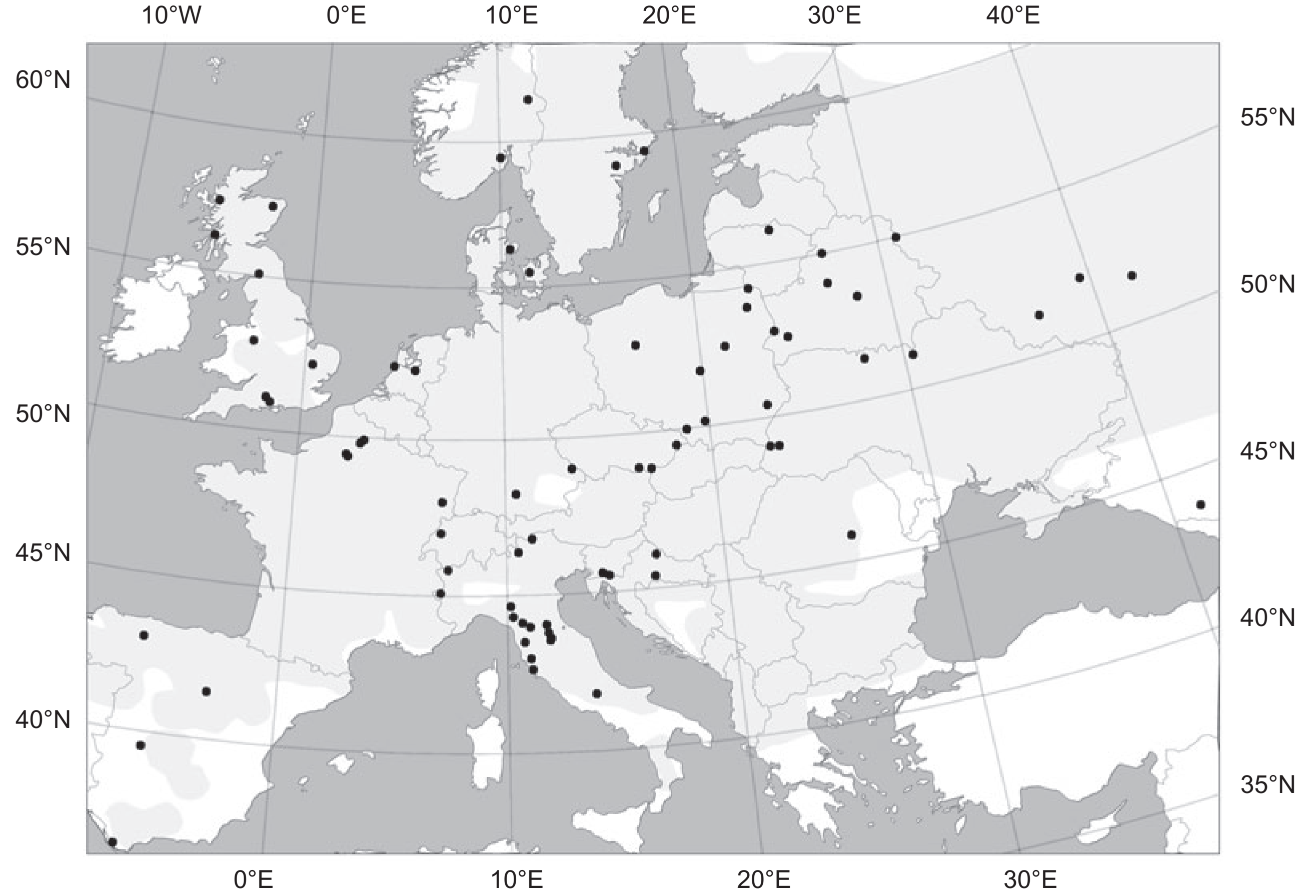

Figure 1 Distribution of analysed data on population density values of roe deer (points) with the range of occurrence of the species in Europe in the background (shaded area; after Geptner *et al.*, 1961; Mitchell-Jones *et al.*, 1999). A list of the data and sources is given in Table S1.

Mean January temperature, maximum snow depth and duration of snow cover were used as measures of winter severity. The Gaussen index [total precipitation – (2 × mean temperature); after Toïgo *et al.*, 2006] was calculated as a measure of drought in spring (April–May) and summer (June–August). Meteorological data were taken from the Global Ecosystems Database version 2.0 (NOAA National Geophysical Data Center, http://www.ngdc.noaa.gov/). We used the monthly Nimbus-7 SMMR derived global snow cover and snow depth data set (covering October 1978 to August 1987; Chang *et al.*, 1987) and IIASA mean monthly values of temperature and precipitation (covering 1931–60, Leemans & Cramer, 1992). The resolution of these data was 0.5°.

We could not use quantitative data on the impacts of predation, hunter harvest and competition on roe deer abundance because densities of wolf and lynx, hunting quotas and density values of red deer were reported in only a very few of the 72 roe deer study sites. Therefore, we used qualitative (presence–absence) information on wolf, lynx, hunting and red deer for each data point (Table S1).

We examined the collinearity between the explanatory variables by calculating pairwise Pearson's correlation coefficients. Indices of summer and spring drought were highly correlated ($r_p = -0.823$), we therefore decided to retain only one of them (summer, named Drought) in further analyses. Drought was not significantly correlated with either FPAR ($r_p = -0.012$) or forest cover ($r_p = -0.113$). January temperature was highly correlated with maximum snow depth and snow cover duration ($r_p = -0.673$ and -0.669, respectively). Thus, we performed a principal components analysis of winter variables (January temperature, maximum snow depth, mean number of months with snow cover). The first component, which explained 72.4% of variance, was negatively correlated with temperature and positively with the two indices of snow. We then used it as an explanatory variable (Winter) in the models to avoid multicollinearity (Graham, 2003). Higher values of the winter index correspond to harsher winter conditions. Other variables (winter and drought, $r_p = 0.455$; winter and forest cover, $r_p = 0.231$; winter and FPAR, $r_p = -0.229$) were not as strongly correlated. The highest correlation was between FPAR and forest cover ($r_p = 0.626$); however, we decided to use both of them as explanatory variables, because they provided different estimates of food abundance for roe deer. The FPAR index can be interpreted as a proxy for overall productivity of vegetation cover, changing in a large, geographical scale. Percentage forest cover shows which relative proportion of the total production of green biomass in a local scale is allocated to tree canopies (unavailable to roe deer).

We used mixed linear models (Pinheiro & Bates, 2000) to analyse the effect of the above listed explanatory variables on roe deer population density. The dependent variable (number of roe deer per 100 km^2) was log-transformed to improve normality and reduce skewness. A likelihood ratio based R^2 (Nagelkerke, 1991) was used as a measure of explained variation in the mixed models, according to the formula

$$R_{\mathrm{LR}}{}^2 = \{1 - \exp[-2n^{-1}(L_{\mathrm{M}} - L_0)]\}/[1 - \exp(-2n^{-1}L_0)],$$

where L_{M} is the log-likelihood of the model of interest, L_0 is the log-likelihood of the intercept-only model and n is the number of observations.

We considered two model designs. First, using the main effects of all variables, we investigated the general pattern of roe deer response. Second, to assess whether the effects of the environmental variables on roe deer differed between populations with different impacts of large predators, we included interaction terms of large predator presence/absence (wolf and/or lynx pooled) with FPAR, forest cover and winter. In both cases, we fitted mixed linear models (using maximum likelihood) to all combinations of variables and performed a model selection using the Akaike information criterion (AIC) with a second-order correction for small sample sizes (AIC$_c$) (Burnham & Anderson, 2002). Since there was not much support for a single best model, we chose a confidence set of models for which ΔAIC$_c$, i.e. the difference in AIC$_c$ between a given model and the best model, was ≤4 and we utilized model averaging to get averaged coefficients and 95% confidence intervals (Burnham & Anderson, 2002). We also calculated the relative importance of each explanatory variable as a sum of Akaike weights across all the models in the confidence set that contained that variable (Burnham & Anderson, 2002).

Diniz-Filho *et al.* (2008) stressed that the AIC is sensitive to the presence of spatial autocorrelation and may generate unstable and overfitted minimum adequate models to describe macroecological data. Therefore, we ran a Mantel test (Legendre & Legendre, 1998) to check for spatial autocorrelation in roe deer abundance and found a positive correlation (Mantel $r = 0.267$, $P < 0.001$). We accounted for this autocorrelation by incorporating a spatial correlation structure in the mixed model (Pinheiro & Bates, 2000). From different classes of spatial structure (see Legendre & Legendre, 1998), we chose an exponential structure, based on the shape of the model's semi-variogram and AIC$_c$. Spatial correlations of each model were estimated with correlograms, calculating Moran's I for model residuals at distance classes of 100 km (see, e.g., Diniz-Filho *et al.*, 2003).

We also checked for the differences between density assessment methods. For this purpose we utilized a generalized additive model (Hastie & Tibshirani, 1990) with latitude and longitude (to account for large-scale patterns) as a smooth term and the method factor as a parametric term. Since the differences between methods of roe deer density assessment were significant ($F = 2.21$, $P = 0.03$), the method was included in the mixed linear models as a random factor (Pinheiro & Bates, 2000). All statistical analyses were conducted using R version 2.8.0 software (R Development Core Team, 2008).

RESULTS

The observed variation in roe deer population density across Europe was very large: the lowest (11 individuals per 100 km^2) and the highest recorded values (5380 individuals per 100 km^2) spanned three orders of magnitude (see Table S1). The abundance of roe deer did not show any consistent latitudinal gradient ($R^2 = 0.02$, $n = 72$, $P = 0.97$), but declined significantly towards the east ($R^2 = 0.26$, $P < 0.002$).

Inclusion of both the census method as a random factor and the correlation structure in the mixed models greatly reduced the small-scale spatial autocorrelation: in the full model ($n = 72$ localities), Moran's I coefficient in the distance class ≤100 km decreased from 0.82 ($P = 0.001$) to 0.11 ($P = 0.17$).

Analysis of large-scale patterns in roe deer density yielded the confidence set of eight models including four to six independent variables and explaining 56–58% of the observed variation (Table 1). Four variables appeared in all models of the confidence set and had the highest relative importance: vegetation productivity, forest cover, presence/absence of lynx and presence/absence of wolf. In the averaged model (Table 2), four variables had significant impacts on roe deer: their population density increased with growing vegetation productivity and declined with increasing forest cover and in localities with lynx and wolf present. The other variables (hunting, winter harshness, summer drought and presence of red deer) had no significant effects on roe deer abundance (Table 2).

The negative effect of predation on roe deer populations was clear: the mean density of roe deer in localities with no large predators was 1485 individuals per 100 km^2 (SE 192, $n = 36$), compared with 605 individual per 100 km^2 (SE 172, $n = 36$) in sites with large predator presence. Moreover, the limiting effect of two co-occurring species of predators (wolf and lynx) was still stronger than that exerted by one species. In sites with one species of large predator present (in most cases wolf), the population density of roe deer averaged 917 individuals per 100 km^2 (SE 276, $n = 21$), whereas populations subjected to both wolf and lynx predation had a mean density of 167 individuals per 100 km^2 (SE 45, $n = 15$). The difference in density between harvested and unharvested roe deer populations was indeed smaller: harvested populations had, on average, 981 individuals per 100 km^2 (SE 164, $n = 52$) and unharvested ones 1213 individuals per 100 km^2 (SE 261, $n = 20$).

Next, we checked whether there were any significant interactions between the effects of environmental variables and predation in shaping roe deer numbers. Significant interaction would suggest that the impact of predators changes along the gradient of environmental features. The model selection performed with models including the interactions of environmental variables

Table 1 Confidence set of mixed linear models ($\Delta AIC_c \leq 4$) with roe deer population density (log-transformed) as dependent variable and vegetation productivity (FPAR index), percentage forest cover (VCF index), winter harshness index (the first PCA component of January temperature, maximum snow depth and mean number of months with snow cover), summer drought [total precipitation − (2 × mean temperature), in June–August] and presence or absence of wolves, lynx, red deer and hunting as explanatory variables.

Variables included in a model	k	R^2	ΔAIC_c	ω_i
Productivity, Forest, Lynx, Wolf	8	0.56	0	0.22
Productivity, Forest, Lynx, Wolf, Hunting	9	0.57	1.18	0.12
Productivity, Forest, Lynx, Wolf, Winter	9	0.57	2.11	0.08
Productivity, Forest, Lynx, Wolf, Drought	9	0.56	2.43	0.06
Productivity, Forest, Lynx, Wolf, Red deer	9	0.56	2.46	0.06
Productivity, Forest, Lynx, Wolf, Hunting, Winter	10	0.58	2.95	0.05
Productivity, Forest, Lynx, Wolf, Hunting, Red deer	10	0.58	3.41	0.04
Productivity, Forest, Lynx, Wolf, Hunting, Drought	10	0.57	3.58	0.04

FPAR, fraction of photosynthetically active radiation; VCF, Vegetation Continuous Fields; PCA, principal components analysis.

k, number of parameters (number of estimated parameters, in addition to the listed number of independent variables, fixed effect and error term, includes also one parameter for random effect 'Method' and an additional two for spatial correlation structure).

R^2, likelihood ratio based coefficient of determination.

ΔAIC_c, difference in corrected Akaike information criterion (AIC_c) between a given model and the best model.

ω_i, Akaike weights.

The models are ordered according to the corrected Akaike Information Criterion (AIC_c) with the most parsimonious model at the top of the list.

Table 2 Relative importance of independent variables and averaged coefficients for the confidence set of most parsimonious models predicting roe deer population density ($n = 8$, $\Delta AIC_c \leq 4$), with unconditional standard error and 95% confidence intervals.

Variable	Relative importance in the confidence set of models	Mean coefficient ± SE	95% confidence intervals Lower	95% confidence intervals Upper
Intercept	–	4.48 ± 0.79	2.93	6.03
Productivity	1	0.06 ± 0.02	0.03	0.10
Forest	1	−0.03 ± 0.01	−0.05	−0.01
Lynx	1	−1.09 ± 0.38	−1.83	−0.35
Wolf	1	−0.79 ± 0.31	−1.39	−0.18
Hunting	0.41	0.16 ± 0.24	−0.30	0.62
Winter	0.19	0.02 ± 0.04	−0.06	0.09
Drought	0.15	0.001 ± 0.003	−0.01	0.01
Red deer	0.15	−0.02 ± 0.06	−0.14	0.10

Variables with significant effects (not spanning 0 within 95% CIs) are in bold.

and presence of large predators yielded the confidence set of 15 models with four to nine independent variables, explaining 57–66% of the observed variation (Table S2). The model averaging led to results consistent with the previous analysis (Table 3). In addition, it showed a significant effect of the interactions between predation and productivity and predation and winter harshness. The interaction between forest cover and predation was not significant.

Based on the model averaged coefficients shown in Table 3, we quantified the effects of the three most important factors (vegetation productivity, winter harshness and forest cover) on roe deer population density across Europe in contrasting situations of presence and absence of large predators (Fig. 2). When wolves and/or lynx are present, roe deer not only occur at lower densities, but the limiting effect of predation becomes notably stronger in areas of low productivity (the two regression lines have different slopes and the difference between them gets larger with decreasing vegetation productivity). The same finding applied to the gradient of winter severity: the limiting effect of predation on roe deer abundance greatly increases in regions with harsh winters, while in the absence of large predators (i.e. the main effect of winter) the relationship was not significant. When forest cover is taken into account, roe deer occur at lower numbers in localities with predators, but the negative relationships between deer abundance and forest cover does not markedly differ between the two situations (both regression lines have the same slopes) (Fig. 2).

We used the empirical relationships revealed by the European-scale analysis to present a graphical model of how bottom-up and top-down forces influence roe deer population abundance (Fig. 3). Within the gradient of environmental productivity ranging from boreal forests, to temperate deciduous woodlands,

Table 3 Relative importance of independent variables and averaged coefficients for the confidence set of most parsimonious models ($n = 15$, $\Delta AIC_c \leq 4$, listed in Table S2) predicting roe deer population density, including interactions of large predator presence (Predation) with environmental variables (Productivity, Forest and Winter), with unconditional standard error and 95% confidence intervals.

Variable	Relative importance in the confidence set of models	Mean coefficient ± SE	95% confidence intervals	
			Lower	Upper
Intercept	–	6.33 ± 1.08	4.19	8.47
Productivity	1	0.04 ± 0.02	−0.01	0.08
Forest	1	−0.04 ± 0.01	−0.06	−0.02
Predation	1	−4.67 ± 1.41	−7.48	−1.86
Winter	0.89	−0.30 ± 0.17	−0.03	0.70
Predation × Winter	0.89	−0.48 ± 0.23	−0.93	−0.03
Predation × Productivity	0.84	0.07 ± 0.03	0.01	0.13
Red deer	0.71	−0.42 ± 0.36	−1.13	0.29
Hunting	0.36	0.18 ± 0.26	−0.33	0.70
Drought	0.35	−0.01 ± 0.01	−0.03	0.02
Predation × Forest	0.16	0.00 ± 0.00	−0.01	0.01

Variables with significant effects (not spanning 0 within 95% CIs) are in bold.

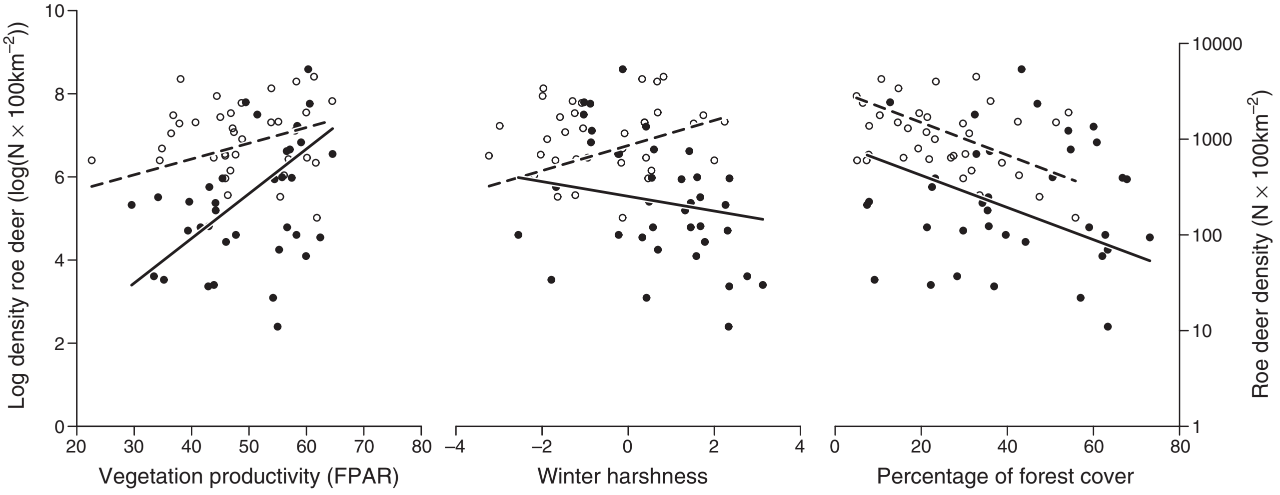

Figure 2 Roe deer density (individuals per 100 km^2, log-transformed) in relation to vegetation productivity index [fraction of photosynthetically active radiation (FPAR) index; left graph], winter harshness [the first principal components analysis (PCA) component of January temperature, maximum snow depth and mean number of months with snow cover, middle graph] and percentage forest cover (right graph). Localities with no large predators are represented by open points, broken lines; localities with lynx and/or wolf present are represented by solid points, thick lines. The lines and equations are based on the averaged model (shown in Table 3). The variables not shown in the graphs were held constant at their mean values. See Table 1 for an explanation of the independent variables.

to the Mediterranean coastal areas, the average population density of roe deer in the absence of predators varied by a factor of three to four, and the increase was nearly linear (Fig. 3). However, when one or two species of predators were present, roe deer numbers reached only a fraction of the numbers attained in a predator-free situation, a fraction that was particularly small (below 10%) in the least productive biomes and notably higher (up to 60–80%) in the most productive ones (Fig. 3). When subject to predation impact, roe deer population abundance varied along the same gradient of productivity by a factor of 40, and showed an exponential increase in the environments with moderate and high vegetation productivity.

DISCUSSION

Based on generalization of a large number of empirical observations (roe deer density values throughout a vast part of their geographical range), we were able to find patterns in roe deer abundance in relation to predator presence, vegetation productivity, forest cover and winter harshness. Other factors that were likely to have influenced our studied populations but could not have been quantified in this analysis include, among others, quantitative measures of hunter harvest intensity, varying management regulations, patterns of forest management and agricultural crop production, the degree of supplementary winter

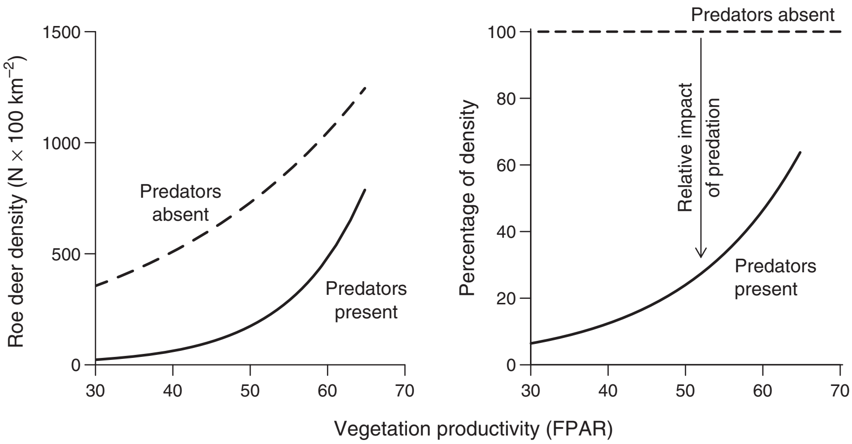

Figure 3 Graphical model explaining the combined top-down and bottom-up control of roe deer population density in Europe. Left graph: mean density of roe deer along a productivity gradient in situations with predation and with no predation impact. Lines are mathematically derived from the regression equations shown in Fig. 2. Right graph: generalized role of predation in limiting roe deer abundance below the habitat carrying capacity along the productivity gradient. The mean density attained when subject to predation (lower line in the left graph) was presented as the percentage of densities with no predation impact.

feeding, the impact of other predators such as feral dogs, *Canis familiaris*, and red foxes, *Vulpes vulpes* (Panzacchi *et al.*, 2008), and population history (long established or recently colonizing). These could all have contributed to an unexplained part of the observed variation in roe deer abundance. Given a plethora of abiotic and biotic, natural and human-related agents acting on roe deer occurrence and numbers, the result obtained in this study (about 56% of the observed large-scale variation in abundance explained by four variables, and up to 66% if the interactions between predation and environmental variables were taken into account) revealed a rather robust biogeographical pattern in roe deer population density in Europe. In the further discussion, we endeavour to identify the causal mechanisms underlying the described pattern.

Recently, Sinclair & Krebs (2002) postulated that, for most herbivore species, bottom-up control (through food supply) is the universal primary standard, which can be modified by secondary factors, such as top-down limitation from predation, social interactions and disturbances. In their analysis of different combinations of these primary and secondary processes, Sinclair & Krebs (2002) focused on interspecific differences (comparing marsupials, ungulates and lagomorphs) and not on intraspecific variation taking place along geographical gradients.

Our study yielded support for the prediction that environmental productivity is decisive for determining population density for roe deer, and we propose that the causal mechanism underlying the observed pattern is regulation by competition for food. Food supply has been shown to be a key factor in the dynamics of roe deer populations in areas as diverse as France and Sweden, affecting the winter body mass of fawns in a density-dependent manner (Pettorelli *et al.*, 2003; Kjellander *et al.*, 2006). Though we were not able to use direct measures of food supply at the biogeographical scale, we believe that the two surrogate indices, FPAR index and percentage forest cover, appropriately reflect the varying availability of food resources to roe deer. Pettorelli *et al.* (2006) successfully correlated remote sensing derived productivity indices with roe deer body mass, but underlined the need for caution. In our study, the FPAR index can be interpreted as a proxy for overall productivity of vegetation cover. However, in the case of forests, most of the green biomass production is allocated to tree canopies and only a small fraction to ground layer vegetation. In more open areas, a higher proportion of overall plant productivity is allocated to ground vegetation (herbs, grass and low shrubs) and thus it is available to roe deer. For example, in a temperate zone of central Europe, productivity of ground vegetation averaged 615 kg of dry mass per ha per year (SE 124) in mixed and deciduous forests, whereas it was 10 times higher (mean 7243 kg, SE 1495) in open grasslands (after Jędrzejewski & Jędrzejewska, 1996). Therefore, sparser forest cover actually implies a greater food supply for roe deer. Similarly, Gill *et al.* (1996) showed that roe deer are better adapted to exploit early successional stages rather than continuous areas of closed-canopy forest. Tixier *et al.* (1996) concluded that closed forest – habitat lacking ecotones – is less favourable for roe deer. Thus, the consistent results of our analyses of the two indices (higher FPAR index and lower forest cover resulting in higher abundance of roe deer) lend weight to the argument that both factors are related to food supply, with FPAR reflecting variation at the biogeographical scale and forest cover at the local scale. Yet, the correlation between these two variables makes it difficult to entirely tease apart their effect on roe deer.

A novel finding of our analysis is that the importance of top-down control for roe deer populations is highly context dependent. In accordance with the predictions by Jędrzejewska & Jędrzejewski (2005) derived from a long-term study on a single population, stronger limitation by predation occurred in less productive environments. A heavy impact of predation on roe deer (by Eurasian lynx and/or by wolves) has been documented in the local studies performed in Switzerland, Poland, Italy and Norway (Okarma *et al.*, 1997; Jędrzejewski *et al.*, 2002; Molinari-Jobin *et al.*, 2002; Odden *et al.*, 2006; Gazzola *et al.*, 2007). Furthermore, it was documented by the analysis of long-term, local data that predators are capable of limiting roe deer numbers markedly below the habitat carrying capacity (Jędrzejewska & Jędrzejewski, 1998). Also, the additive effects of the two studied species of large carnivores were documented in a study conducted at a local scale (eastern Poland; Jędrzejewska & Jędrzejewski, 1998).

The causes of productivity-related differences in top-down limitation may lie in the characteristics of both predator and prey. First, studies conducted at a local scale (Białowieża Forest, Poland) have documented that the percentage of predation on roe deer is inversely density dependent: heavier at low than at high densities of prey (Jędrzejewska & Jędrzejewski, 1998). At the geographical scale, kill rates by Eurasian lynx only vary by a factor of two across a range of prey densities spanning two orders of magnitude (Breitenmoser & Haller, 1993; Linnell *et al.*, 1996; Okarma *et al.*, 1997; Molinari-Jobin *et al.*, 2002) implying that predation rate can be high at low prey density, despite the fact that territory sizes of lynx and wolves decline with growing prey density and productivity (Herfindal *et al.*, 2005; Nilsen *et al.*, 2005; Jędrzejewski *et al.*, 2007; but see Molinari-Jobin *et al.*, 2007). This study is therefore an indication that inverse density-dependent predation (see Messier, 1995) may also occur at large spatial scales.

Secondly, it could be expected that roe deer populations in more productive environments may be better able to compensate for predation through more rapid population growth rates. However, recent analysis of the demographic parameters of roe deer across a wide range of populations does not support this idea as there are no obvious biogeographical gradients in survival or recruitment (Nilsen *et al.*, 2009). In fact, the northernmost populations have the largest litter sizes at birth (Andersen *et al.*, 1998b).

Numerous investigations have documented that roe deer survive well and have even increased their range and densities in northern environments (review in Holand *et al.*, 1998) during recent decades. By comparison, population abundance of wild boar, *Sus scrofa* L., which do not occur as far north as roe deer (Mitchell-Jones *et al.*, 1999), critically depends on winter temperatures (Melis *et al.*, 2006). However, very severe winters with deep snow cover can be a major cause of density-independent mortality in roe deer populations as well (Okarma *et al.*, 1995; Danilkin, 1996). The significant effect of winter severity on roe deer abundance, found in our analysis only in localities with large predators, strongly suggests that in northern regions, mortality caused by unfavourable winter conditions and that caused by predators are likely to be additive rather than compensatory.

Competition with red deer did not appear to play a limiting role for roe deer abundance at the biogeographical scale. In local studies, competition with red deer was documented in a high-density, predator-free population of roe deer in Scotland (Latham *et al.*, 1996), but not in a low-density, predation-limited population in eastern Poland (Jędrzejewska *et al.*, 1997). Understanding the factors that modulate the impacts of red deer on roe deer is a topic deserving future study. Although summer drought has been identified as an important factor affecting some roe deer populations in some years (Toïgo *et al.*, 2006), it did not appear as a significant factor at the scales examined in this study. This could be due to the diversity of local influences that can modulate the impact of summer drought.

The lack of support for a limiting role of hunter harvest in shaping roe deer densities at a continental scale may at first seem counterintuitive, as wildlife managers tend to believe that hunting substantially reduces deer population density. This has indeed occurred in some localities (e.g. Dourdan, France; Vincent *et al.*, 1995), while in other places (e.g. Białowieża Forest, Poland, in 1960–90; Jędrzejewska *et al.*, 1997) hunting harvest had no significant effect on fluctuations in roe deer numbers. Generally, the fact that most European populations of roe deer have long been subjected to hunter harvest but nonetheless have been increasing in numbers in the recent decades (Andersen *et al.*, 1998a) corroborates our conclusion that, at the continental scale, hunting has generally had a very modest influence on roe deer abundance.

The results of our study are consistent with the conclusions of Wang *et al.* (2009), who performed a meta-analysis of 23 time series (covering from 19–74 years) of abundance estimates of 13 species of northern ungulates to reveal how density dependence in population fluctuations interacts with resources and predation. They found that the strength of density dependence in ungulate populations was low in the presence of large predators, particularly at northern latitudes with low primary productivity.

Interestingly, the single local study that has compared the effect of a similar set of factors (temperature, predation, intra- and interspecific competition) on roe deer abundance and rates of population increase in Białowieża Primeval Forest, eastern Poland yielded results compatible with those revealed by our European-scale study: predation by lynx was the essential factor, intra-specific competition and mean annual temperature were less important and competition with other wild ungulates was insignificant (Jędrzejewska *et al.*, 1997; Jędrzejewska & Jędrzejewski, 1998, 2005).

In conclusion, we have shown that, in Europe, the population density of roe deer has been shaped by both bottom-up (food related) and top-down (predators) factors. Top-down control became stronger with declining environmental productivity and increasing harshness of winter. We proposed that the causal understanding of the described patterns may lie in one or more of the following mechanisms: (1) the inverse density dependence of the impact of predation; and (2) the additive character of predator-caused and winter-caused mortality of roe deer in harsher regions.

Finally, the results of our large-scale analysis have clear implications for conservation and management of roe deer populations in Europe. Firstly, we may expect that changes in environmental productivity caused by climatic warming (Nemani *et al.*, 2003) will drive subsequent changes in roe deer abundance. Secondly, the discussion on recovery and reintroduction of large predators (especially lynx, e.g. Hetherington,

2006) should consider the fact that their expected effect on roe deer numbers will depend on environmental productivity. As predicted by our model (see Fig. 3), in the most productive regions, that limitation may attain –20% to –40% of the predator-free population density. In the least productive regions, the impact of lynx or wolves may reach the level regarded by wildlife managers as devastating for the local roe deer population.

ACKNOWLEDGEMENTS

The work was supported by the project BIOTER-Centre of Excellence in Biodiversity Conservation and Mammal Research financed by the European Commission (5FP, EVK2-CT-2002-80011). Additional funds were provided by a CNR-NATO fellowship (no. 215.36) to C.M., the Research Council of Norway, and the Polish Ministry of Science and Higher Education, grant no. 2 P04F 028 29. We are grateful to Dr S. Lovari for his help with the literature data search for the Mediterranean region. Drs M. Hewison, J.-M. Gaillard and two anonymous referees made helpful comments on our manuscript. We thank all researchers and wildlife managers who kindly provided information about the hunting status of roe deer populations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 List of data and sources used in this paper.

Table S2 Confidence set of mixed linear models ($\Delta\text{AIC}_c \leq 4$; AIC_c is the corrected Akaike information criterion) with roe deer population density as the dependent variable, environmental variables and interactions between environmental variables and predation as explanatory variables.

BIOSKETCHES

Claudia Melis has done her PhD on the territorial behaviour of roe deer. She is interested in the biogeographical variation in ungulate densities and the effects of invasive species on communities.

Marco Apollonio is specialized in the behavioural ecology and conservation biology of European ungulates (roe deer, red deer, fallow deer, wild boar and ibex) and wolves. He has also studied various aspects of molecular ecology and systematics of large mammals, and is interested in pan-European diversity in wildlife management.

Bogumiła and **Włodzimierz Jędrzejewski** have conducted long-term studies on predator–prey relationships and population regulation of vertebrates in Poland. They are interested in large-scale variation and patterns in animal population ecology and genetics. They initiated this collaboration of European researchers on meta-analysis of data on ungulates and large carnivores aimed at elucidating the role of bottom-up and top-down forced in shaping the populations densities of large mammals.

Editor: Mikko Mönkkönen